

Poecilogony and larval ecology in the gastropod genus *Alderia**

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Abstract: The gastropod genus *Alderia* (Allman, 1845) (Opisthobranchia: Sacoglossa) contains a rare case of poecilogony, or variable larval development within a species. This paper reviews the alternative larval morphs and dispersal strategies expressed by *Alderia* spp., and presents new data on larval ecology, environmentally induced changes in development, and rates of metamorphosis for larvae differing in age and life history. Recent morphological and molecular analyses revealed a cryptic poecilogonous species in the previously monotypic genus *Alderia*. The newly described *Alderia willowi* Krug *et al.*, 2007 occurs south of Bodega Harbor, California, and was the subject of all prior studies by Krug and co-workers. Unlike its strictly planktotrophic congener *Alderia modesta* (Lovén, 1844), *A. willowi* produces either small feeding larvae that have a 30-day pre-competent period or large larvae that need not feed to metamorphose. Individuals can vary the developmental mode of their offspring, with a variable proportion switching from lecithotrophy (prevalent in summer) to planktotrophy in winter or spring; a similar shift is induced in some adults upon transfer to the laboratory. In a second dispersal polymorphism, a variable percentage of lecithotrophic larvae undergo spontaneous metamorphosis within 2 days of hatching, while their siblings disperse until induced to settle by carbohydrate cues from the host algae *Vaucheria* spp. The percentage of spontaneous metamorphosis is uncorrelated with fecundity and is generally between 15-30%, a possible product of stabilizing selection on this bet-hedging dispersal strategy. Despite their different ages, competent larval morphs produced by alternative developmental pathways are similar in size, swimming behavior, and responses to dissolved settlement cues. However, competent planktotrophic larvae and older lecithotrophic larvae initiated metamorphosis faster after settlement than newly hatched lecithotrophic larvae, suggesting a link between planktonic period and habitat choice. Although rare, poecilogonous species like *A. willowi* offer special insights into the evolutionary causes and ecological consequences of alternative life histories.

Key words: bet-hedging, cryptic species, dispersal polymorphism, larval settlement, sacoglossan

A major difference between marine and terrestrial life histories is the dichotomy between feeding and non-feeding modes of larval development among marine invertebrates (Strathmann 1990, 1993). Most species produce either a large number of small larvae that must feed in order to attain competence (planktotrophy) or fewer, larger larvae that can metamorphose without feeding (lecithotrophy) (Wray and Raff 1991, Levin and Bridges 1995). Ecologically similar and related species often differ in developmental mode for reasons that remain unclear, and there is no theory specifying which selective regimes should favor lecithotrophy over planktotrophy (Todd *et al.* 1998, McEdward 2000). Phylogenetic studies have demonstrated that transitions between developmental modes have occurred numerous times in diverse groups such as molluscs (Duda and Palumbi 1999, Meyer 2003, Collin 2004), echinoderms (Hart *et al.* 1997, Hart 2000, Jeffrey *et al.* 2003), and urochordates (Hadfield *et al.* 1995). Planktotrophy is presumed to be ancestral to lecithotrophy because complex feeding structures, once lost, are rarely regained via adaptive evolution (Strathmann 1978,

1985, 1993, Wray 1995). Both the fossil record and phylogenetic hypotheses generally support this one-way trend towards non-planktotrophic development (Hansen 1982), although species with nurse eggs may be an exception (Collin 2004). The forces that drive transitions to non-feeding larvae are poorly understood, however, and the dearth of intermediate stages or organisms expressing multiple forms of development within a species have impaired attempts to understand this aspect of life-history evolution.

Although causal explanations remain elusive, the ecological and evolutionary consequences of different developmental strategies are profound (Perron 1986, Pechenik 1999). The paleontological record for molluscs indicates that species with planktotrophic larvae have greater geological longevity and broader geographical ranges than those exhibiting lecithotrophy, which speciate at a higher rate (Hansen 1978, 1980, 1982, Jablonksi 1986). Species with lecithotrophic or direct development are more prone to extinction, but often show greater local adaptation (Hansen 1978, Sanford *et al.* 2003). The prolonged pelagic period of most feeding larvae makes them effective vectors for gene flow, and planktotrophic taxa generally exhibit panmictic populations (Palumbi 1995, Caley *et al.* 1996). The continuous influx of alleles from distant populations can prevent planktotrophic species from adapting to local conditions (Vermeij 1982).

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Intraspecific phylogeographic breaks occur in planktotrophic species but are usually small in magnitude compared to the highly structured populations often observed within species that have non-feeding larvae with reduced dispersal potential (Kyle and Boulding 2000, Wares *et al.* 2001, Collin 2003).

An improved understanding of how selection drives developmental evolution may come from studies of rare species that display intraspecific polymorphism in larval development. Termed "poecilogony", this phenomenon appears perplexingly restricted to spionid polychaetes and opisthobranch molluscs (Giard 1905, Hoagland and Robertson 1988, Bouchet 1989, Chia *et al.* 1996). Molecular studies discredited other purported examples of variable development as cryptic species. True cases of poecilogony can inform as to the ecological significance of alternative dispersal strategies (Levin 1984a, Levin and Huggett 1990, Levin and Bridges 1994), and may indicate when natural selection favors one larval mode over another. Such species may also provide insight into the mechanisms underlying developmental transitions, such as allocation of maternal resources and gene expression (Villinski *et al.* 2002, Marsh and Fielman 2005).

Some opisthobranchs have been classified as poecilogonous because offspring can metamorphose either before or after hatching from benthic egg masses. These may be more constructively termed "dispersal polymorphisms"; they do not constitute variable development as there is no difference in egg size or larval trophic mode. Such dimorphisms can result if the egg mass matrix retains or releases larvae according to season (e.g., *Elysia timida* Risso, 1818; Marin and Ros 1989), adult nutritional state (*Tenellia adspersa* Nordmann, 1845; Chester 1996), or experimental conditions (*Berghia verrucicornis* Costa, 1864; Carroll and Kempf 1990). In the cephalaspidean *Haninaea callidegenita* Gibson and Chia, 1989, some larvae attain competence prior to hatching and undergo intracapsular metamorphosis triggered by an inducer in the egg jelly, while siblings become competent after hatching and settle in response to benthic biofilms (Gibson and Chia 1989). Dispersal polymorphisms can also result from differences in settlement cue requirements among pelagic larvae (Mackay and Doyle 1978, Raimondi and Keough 1990, Toonen and Pawlik 1994), but this has received little attention as a potentially important adaptation in marine life histories.

Truly variable development is expressed in species where developmental mode differs between offspring due to variation in egg size or pre-hatching consumption of nurse eggs or extra-zygotic yolk. In all recognized cases, this involves alternative developmental pathways that produce either feeding larvae that ingest planktonic food after release or larvae that can metamorphose without feeding after re-

lease from parental brood structures or benthic egg masses. One definition of "lecithotrophy" applies to larvae that are incapable of ingesting particulate food (Chia 1974); other definitions include larvae that do not need to feed to complete metamorphosis, whether or not they can (Thompson 1967). The larger larval morph of most poecilogonous species can feed, either by ingesting nurse eggs prior to hatching or facultatively capturing phytoplankton if food is available (Gibson and Gibson 2004, Botello and Krug 2006, Pernet and McArthur 2006). In this review, I use Thompson's (1967) definition of "lecithotrophic."

It is noteworthy that no example of variable development involves a free-spawning organism; among polychaetes, eggs are retained in structures associated with adult tubes, and in sacoglossan opisthobranchs, within benthic egg masses. Although there are reported examples of poecilogony among sacoglossans that include pelagic lecithotrophy and direct benthic development (usually through encapsulated metamorphosis), these likely constitute examples of dispersal polymorphisms as described above, or cryptic species (e.g., "*Elysia cauze*," later recognized as three distinct species; Clark and Goetzfried 1978, Clark 1984, 1994).

Research into poecilogony has been historically confounded by the prevalence of cryptic species in the taxa that contain well-documented examples of variable development, namely polychaetes and opisthobranchs (Grassle and Grassle 1976, Clark 1984, Hoagland and Robertson 1988, Morrow *et al.* 1992, Clark 1994, Chia *et al.* 1996, Schulze *et al.* 2000, Kruse *et al.* 2003). Confirmation of variable development requires molecular data or breeding experiments to demonstrate that individuals differing in larval trophic mode are conspecifics. Among polychaetes, such data exist for *Boccardia proboscidea* (Gibson *et al.* 1999, Gibson and Gibson 2004), populations of *Streblospio benedicti* from the east coast of North America (Levin 1984b, Levin *et al.* 1991, Schulze *et al.* 2000), and *Pygospio elegans* (Morgan *et al.* 1999). Among opisthobranchs in the order Sacoglossa, three poecilogonous species have been confirmed by molecular data or laboratory crosses. In breeding studies, planktotrophic and direct-developing specimens of *Elysia chlorotica* Gould, 1870 from different populations produce viable hybrid offspring (West *et al.* 1984). The Caribbean species *Costasiella ocellifera* Simroth, 1895 was reported as a cryptic species complex (Miles and Clark 2002), expressing planktotrophy or benthic development in different populations, but recent data indicate these populations comprise a single species and that individuals differing in development co-occur and share mitochondrial haplotypes (Ellingson and Krug, unpubl. obs.).

The third example of poecilogony among sacoglossans was reported from southern California among sea slugs in the genus *Alderia* (Allman, 1845), a member of the cerata-

bearing family Limapontiidae (Krug 1998). *Alderia* spp. are specialized herbivores that feed solely upon the algae *Vaucheria* spp. (Ochrophyta: Vaucheriales), found on mudflats in temperate estuaries throughout the northern hemisphere (Trowbridge 2002). The type species *A. modesta* (Lovén, 1844) was described from northern Europe and later reported from both coasts of North America (Engel *et al.* 1940, Hand and Steinberg 1955, Hartog 1959, Bleakney and Bailey 1967, Clark 1975, Vader 1981, Bleakney 1988, Trowbridge 1993, 2002, Martynov *et al.* 2006). Planktotrophy was the sole developmental mode reported from the western Atlantic (Clark 1975), eastern Atlantic (Engel *et al.* 1940, Seelemann 1967), western Pacific (Chernyshev and Chaban 2005), and eastern Pacific as far south as Monterey, California (Hand and Steinberg 1955, Trowbridge 1993, Gibson and Chia 1994). Populations south of Monterey were recently described as a new species *A. willowi* Krug *et al.*, 2007, based on morphology, molecular data, and the expression of both lecithotrophy and planktotrophy (Ellingson and Krug 2006, Krug *et al.* 2007).

This paper will focus on *Alderia* spp., reviewing prior studies that used *A. willowi* as a model to study swimming and settlement behavior of alternative larval morphs and recent work on cryptic speciation in the genus. New data will be presented to address the following research questions: (1) How do reproductive and larval characteristics for the poecilogonous *A. willowi* compare with those of its planktotrophic congener *A. modesta*? (2) Does environment affect the type of larvae produced by *A. willowi*? (3) Does the percentage of spontaneous metamorphosis co-vary with fecundity or does it remain similar across populations of *A. willowi*? (4) Do newly competent planktotrophic larvae show an accelerated rate of metamorphosis similar to that of older lecithotrophic larvae?

MATERIALS AND METHODS

Study sites and taxa

Specimens of *Alderia* spp. and algae were collected at low tide on mudflats from study sites along the west coast of the U.S.A. (Fig. 1). The algal host in southern California is recognized as *Vaucheria longicaulis* (Abbott and Hollenberg 1976); however, this nominal taxon likely comprises a cryptic species complex, as there has been no detailed taxonomic assessment of *Vaucheria* spp. from the northeastern Pacific. I refer to algae from southern California as *V. longicaulis* but, when referring to the whole coast, use *Vaucheria* spp. to reflect taxonomic uncertainty in this genus.

Clutch and larval characteristics of *Alderia* spp.

For *Alderia modesta*, adults were collected in Bodega Harbor, California, in September and October 2004-2005.

Egg masses collected within 8 hr of deposition were isolated in dishes of 0.22- μ m filtered seawater (FSW) until hatching commenced. The diameters of eggs and capsules were measured from high-resolution digital photographs of egg strings removed from the egg mass, calibrating pixel number per μ m with photographs of a hemocytometer grid at the same magnification. Data for planktotrophic and lecithotrophic development in *Alderia willowi* are from Krug (1998).

Changes in developmental mode: field surveys and laboratory experiments

Surveys of developmental mode were carried out in San Diego (1996-1999, 2003-2004), the Upper Newport Bay Ecological Reserve (2003-2004), and a man-made wetland adjacent to the Los Angeles Harbor (2003-2004). Specimens were isolated in petri dishes of seawater for clutch deposition overnight, and clutches were scored for developmental mode 1-2 days later based on egg size (Krug 1998). The proportion of the population producing lecithotrophic clutches was compared for March vs. August of 1996-1999 for San Diego, the only site for which such data were available each year, using a Mann-Whitney *U*-test (as implemented by StatView statistical software package).

Adults collected from Los Angeles were typed for developmental mode of their first clutch (February 2004). Those producing lecithotrophic eggs ($n = 20$) were placed on a patch of *Vaucheria longicaulis* from which all slugs had been removed; algae and slugs were maintained in an incubator at 22 °C on a 14:10 light:dark cycle. Egg masses deposited overnight were collected and typed for developmental mode every 1-2 days for 3 weeks. The proportion of lecithotrophic clutches (y) was regressed against time (x) using a Model 1 regression in StatView.

Spontaneous metamorphosis in clutches of field-collected adults

Adult slugs were collected in San Diego (August 1999), San Francisco (September 2004), and from three sites within Tomales Bay: south Tomales, September 2003; Cow Landing, September 2004, and Walker Creek, September 2004. Slugs were transported to the lab, isolated, and their first clutch harvested. Egg masses were kept in FSW until hatching (5-6 days) and scored for (1) egg number and (2) the percentage of spontaneous metamorphosis occurring in the first 2 days post-hatching (Krug 2001). The null hypothesis of no variation in the percentage of spontaneous metamorphosis between sites was evaluated using a non-parametric Kruskal-Wallis test. A Spearman Rank Correlation test was used to compare fecundity and percentage of spontaneous metamorphosis for the five sites.

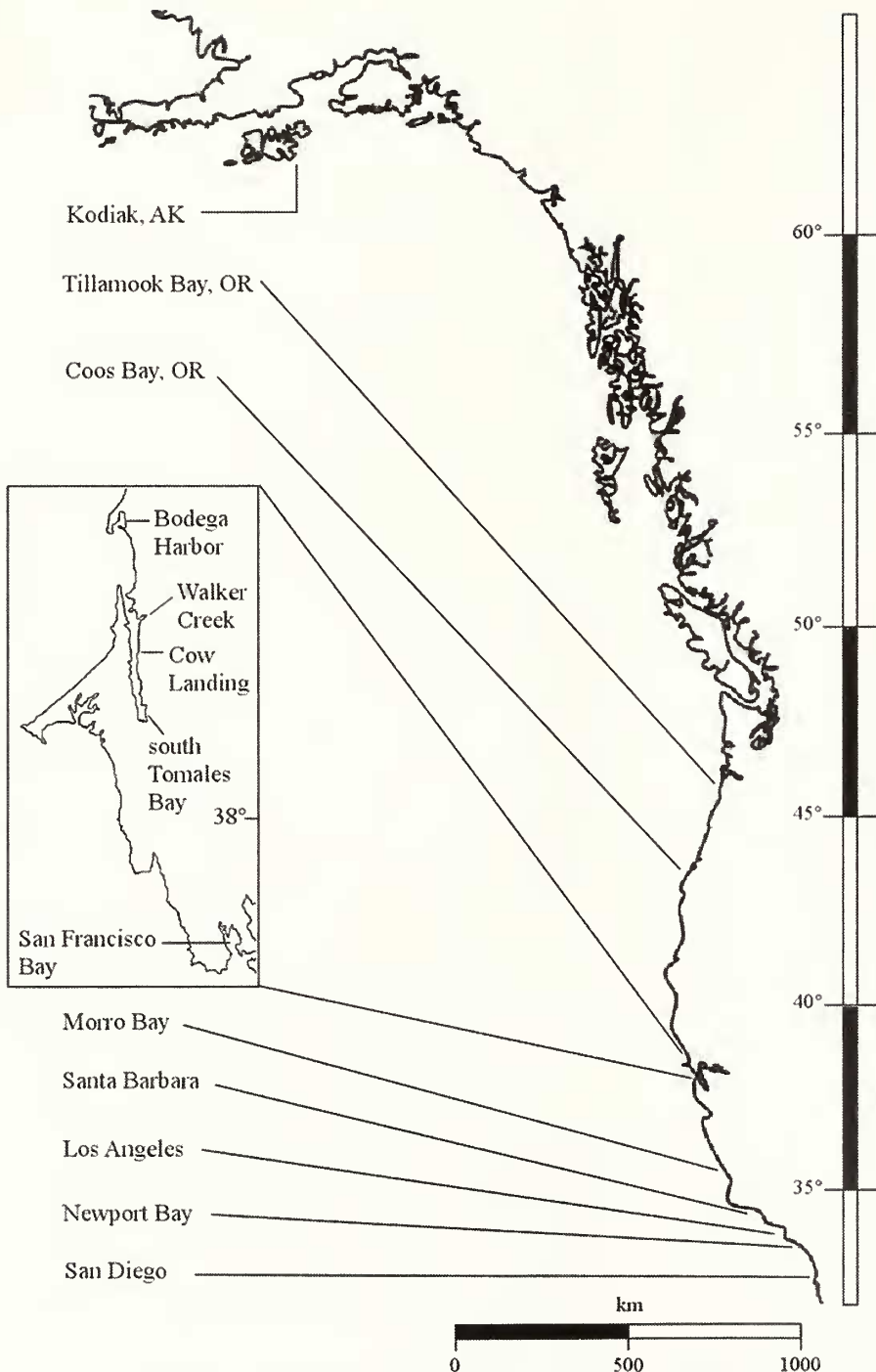


Figure 1. Map of collection sites for *Alderia* spp. from the northeastern Pacific. Inset shows close-up of the area between San Francisco Bay and Bodega Harbor, where both species seasonally co-occur and have their southern (*A. modesta*) or northern (*A. willowi*) range limits.

Rate of metamorphosis in larvae of different ages and developmental modes

Planktotrophic larvae of *Alderia willowi* were cultured as in Krug and Zimmer (2000, 2004) and used in assays after 32 days. Larvae ($n = 15$ per dish, 6 replicates per age class) were exposed to live *Vaucheria longicaulis* and scored for settlement and metamorphosis starting 2 hr after algae were added and at 12 hr intervals thereafter. Settlement is a reversible attachment to the bottom, whereas metamorphosis is an irreversible transformation into a juvenile slug. Cumulative percentages of metamorphosis were not normally distributed after transformation and were, thus, compared after 24 and 48 hr within each age class using a Wilcoxon Signed Rank test; no difference would indicate that most metamorphosis occurred in the first 24 hr whereas a difference would indicate a delayed metamorphic response. These assays were run concurrently with the experiments in Botello and Krug (2006), a study from which data for lecithotrophic larvae of *A. willowi* aged 1, 2 and 4 days post-hatching were taken; the data for planktotrophic larvae were not previously reported.

RESULTS AND DISCUSSION

Poecilogony and cryptic species in the genus *Alderia*

The first report of lecithotrophy in "*Alderia modesta*" was also a southern range extension of ~500 km for this previously monotypic genus (Krug 1998). The global phylogeography of *Alderia* was recently studied by sampling estuaries throughout the northeastern Pacific (Fig. 1), one site in the western Pacific, and one in the eastern Atlantic. Slugs were typed for developmental mode and morphology of the dorsum and radula, and portions of two mitochondrial genes (cy-

tochrome oxidase I (COI) and 16S ribosomal subunit) were sequenced and analyzed (Ellingson and Krug 2006). Most specimens south of Bodega Harbor, California, U.S.A. comprise a poecilogenous cryptic species, *Alderia willowi* (Krug *et al.* 2007). It is distinguished from *A. modesta* by a humped dorsum covered with fused patches of dark pigment (Figs. 2A-B), the seasonal production of lecithotrophic larvae, and the morphology of its radula and egg masses. The congener *A. modesta* occurs seasonally in San Francisco Bay and from Tomales Bay north throughout the Pacific and north Atlantic. *Alderia modesta* has a smooth, speckled dorsum (Figs. 2C-D) and expresses only planktotrophic development.

Molecular data discriminated clearly between the sister species, which form reciprocally monophyletic clades 18-

24% divergent in COI and 2.9% divergent in 16S (Tamura-Nei distances) (Ellingson and Krug 2006). All prior publications by Krug and co-workers on "*Alderia modesta*" in fact concerned its cryptic sister species *A. willowi*. Though nominally conspecific, *A. modesta* from the north Atlantic are substantially divergent (10-12% in COI) from Pacific *A. modesta*. Populations in the two oceans have likely been allopatric since the early Pleistocene, supporting the hypothesis of Bleakney (1988) that trans-Arctic gene flow in *A. modesta* ceased when glaciation covered the Arctic sea. However, given the lack of morphological and developmental differences between ocean basins, *A. modesta* may still be one biological species; breeding studies and further sampling of Atlantic sites are needed to test this hypothesis. Speciation in

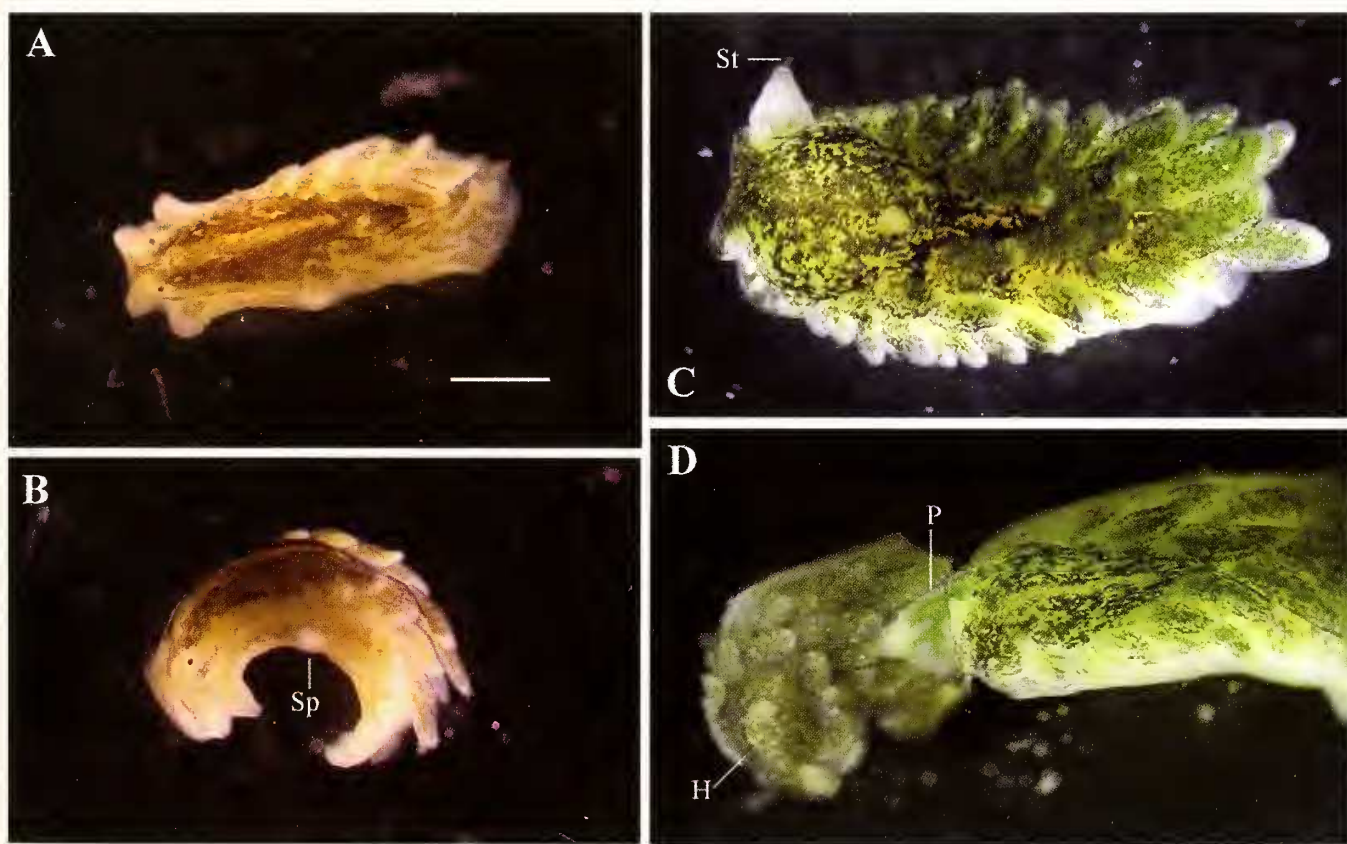


Figure 2. Photographs of individuals of *Alderia* spp. from the northeastern Pacific. A, Dorsal view of *Alderia willowi*, recently described from California. A distinctive morphological feature of this species is that the dorsum is raised into a hump, with a yellow stripe extending down the midline; the dark pigmentation is also fused into continuous patches. B, Side view of the same specimen, which had just been hypodermically inseminated; the white bulge on the foot (Sp) is a subcutaneous sperm deposit. C, Dorsal view of *Alderia modesta*, found on eastern and western coasts of the Atlantic and Pacific. Its dorsum is smooth, often shield-shaped, and covered in speckles of dark pigment. This individual had recently fed on *Vaucheria longicaulis* and the green cytoplasm is visible within digestive diverticula ramifying throughout the body, including the cerata. The penis, extending from the right side of the head, is tipped with a stylet (St) for piercing the body wall of mates during hypodermic insemination. D, Interspecific mating attempt, with a specimen of *A. modesta* probing a smaller specimen of *A. willowi* with its penis (P). Green digestive diverticula can be seen enervating the penis of *A. modesta*. The humped dorsum (H) of *A. willowi* is evident. All photos to same scale; scale bar = 800 μ m.

Table 1. Clutch characteristics of *Alderia willowi*, a poecilonous species occurring south of Bodega Harbor, California, and its planktotrophic congener *Alderia modesta*, which occurs from San Francisco Bay northwards. For *A. willowi*, adults were collected from the Northern Wildlife Preserve in Mission Bay, San Diego, from January to April in 1996 and 1997; planktotrophic and lecithotrophic clutches were reared at 25°C (Krug 1998). Data for *A. modesta* were obtained in September 2005 for specimens from Bodega Harbor. Data are means \pm SD.

	<i>Alderia willowi</i>		<i>Alderia modesta</i>
	Lecithotrophic	Planktotrophic	Planktotrophic
Encapsulated period (days)	5.4 \pm 0.6 (<i>n</i> = 30)	3.0 \pm 0.5 (<i>n</i> = 30)	4.7 \pm 1.2 (<i>n</i> = 18)
Eggs per clutch	32 \pm 12 (<i>n</i> = 30)	311 \pm 134 (<i>n</i> = 30)	463 \pm 117 (<i>n</i> = 15)
Egg diameter (μ m)	105 \pm 5 (<i>n</i> = 328)	68 \pm 4 (<i>n</i> = 517)	78 \pm 4 (<i>n</i> = 75)
Egg capsule diameter (μ m)	247 \pm 31 (<i>n</i> = 328)	121 \pm 12 (<i>n</i> = 517)	127 \pm 10 (<i>n</i> = 75)
Maximum larval shell dimension at hatching (μ m)	186 \pm 9 (<i>n</i> = 282)	116 \pm 8 (<i>n</i> = 160)	124 \pm 8 (<i>n</i> = 45)

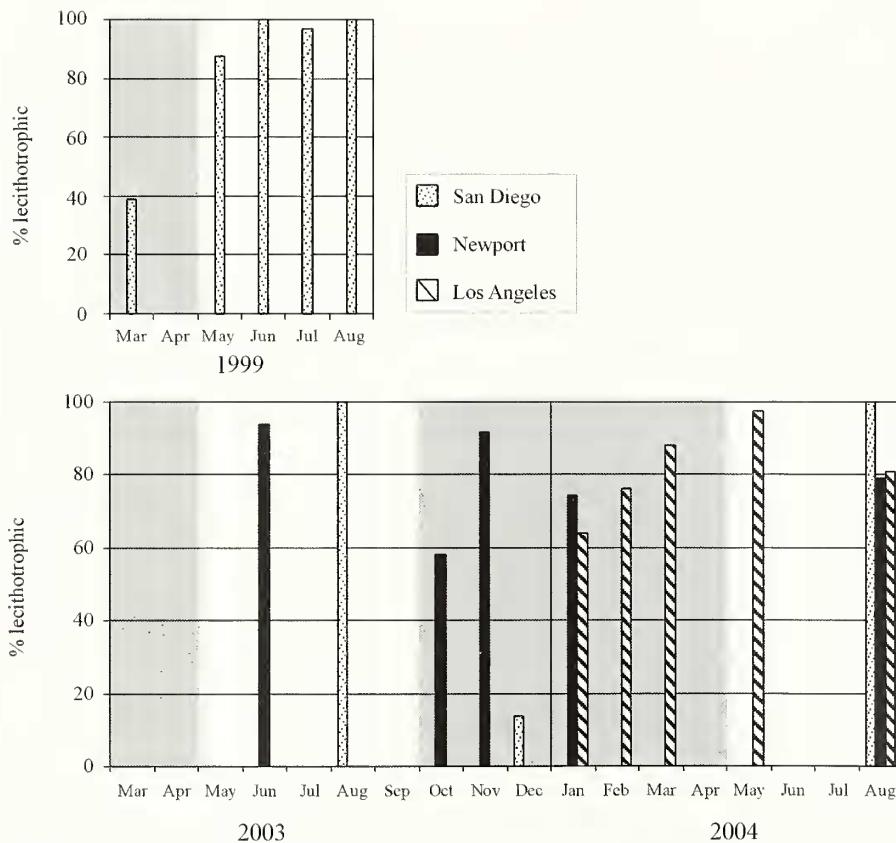


Figure 3. Seasonal variation in the proportion of adult *Alderia willowi* producing lecithotrophic clutches in three southern Californian estuaries. Expression of lecithotrophy generally only drops below 80% from October to April (shaded).

the Pacific pre-dated colonization of the Atlantic, indicating a Pacific origin for the genus *Alderia* (Ellingson and Krug 2006).

Reproductive and larval characteristics of *Alderia* spp.

Developmental data for planktotrophic larvae of *Alderia modesta*, and for both clutch types in *Alderia willowi*, are

given in Table 1. This table is adapted from Krug (1998) to reflect the new species status of *A. willowi* and to include comparative data for the true *A. modesta*. The larger planktotrophic clutches of *A. modesta* took longer to develop and hatch than the smaller planktotrophic clutches of *A. willowi*. Mean adult size was greater for individuals of *A. modesta* (range: 5.5–23.1 mg, *n* = 6 populations) than for *A. willowi* (range: 0.9–5.8 mg, *n* = 6 populations). In both species about 80% of the variance in fecundity is due to adult size (Ellingson and Krug 2006).

Environmentally cued change in development in *Alderia willowi*

Populations of *Alderia willowi* were surveyed in southern California starting in 1996, and showed a consistent seasonal trend. In 1999 (San Diego) and 2003–2004 (3 field sites), clutches were 80–100% lecithotrophic from May–September, but typically less than 80% lecithotrophic from October–April (Fig. 3). The San Diego population had the most extreme shifts; from 1996–1999, the population was 100% lecithotrophic in August

but only 55 \pm 25% SD lecithotrophic in March of those years (Mann-Whitney *U*-test, *Z* = –2.3, *P* < 0.05). The switch to planktotrophy was roughly coincident with seasonal drops in sea-surface temperature and salinity. Populations from Newport Bay and Los Angeles Harbor exhibited a similar trend, but a higher proportion of adults remained lecithotrophic from fall to spring (Fig. 3).

Some slugs expressing lecithotrophy in the field switched to planktotrophy when held in the laboratory for 1-3 weeks (Fig. 4). Adults were maintained on patches of *Vaucheria longicaulis* in the laboratory and laid typical numbers of clutches; the change in their egg size was thus not due to starvation, which can also trigger a switch to planktotrophy (Krug 1998). The proportion of planktotrophic clutches increased over time (Fig. 4, and results of a regression of the effect of time, x , on % planktotrophy, y : $y = -2.80x + 93.69$; $F_{1,9} = 28.18$, $P = 0.0005$, $r^2 = 0.73$). The change in larval type was interpreted as an adult response to the lab environment; reverse transitions to lecithotrophy have not been successfully induced, suggesting the laboratory mimics winter conditions. Siblings reared from the egg under laboratory conditions exhibited either developmental mode and rarely changed between modes (N. Smolensky and P. Krug, unpubl. obs.). Slugs transitioning between development modes in the laboratory sometimes produced clutches of intermediate-sized eggs, first reported in Krug (1998); such clutches are produced by field-collected slugs during transitional months, when the populations are switching either from or towards lecithotrophy (unpubl. data). These data suggest seasonal changes in development reflect changes within individuals, not just between generations within a population.

Together, the evidence suggests that individuals respond to fluctuating conditions by varying their egg size and, hence, mode of development of their larvae. Seasonal shifts in development have not been reported among other poecilogonous species, in which larval type varies by location (West *et al.* 1984, Levin and Huggett 1990, Levin and Creed 1991, Morgan *et al.* 1999, Miles and Clark 2002). There is no other example of a poecilogonous species in which individual adults facultatively change the larval type of their offspring, making *Alderia willowi* a unique model system for investigating the ecological forces and biochemical mechanisms underlying alternative developmental modes.

The life-history strategies of planktotrophy and lecithotrophy substantially alter the hatching characteristics and dispersal potential of larvae. Lecithotrophy doubles the encapsulated period of larvae in *Alderia willowi* and reduces fecundity by an order of magnitude (Table 1). However, lecithotrophic larvae are competent to metamorphose even before hatching (Krug 2001, Botello and Krug 2006), reducing their total development time from about 35 days (planktotrophy) to 5 days and presumably decreasing larval mortality.

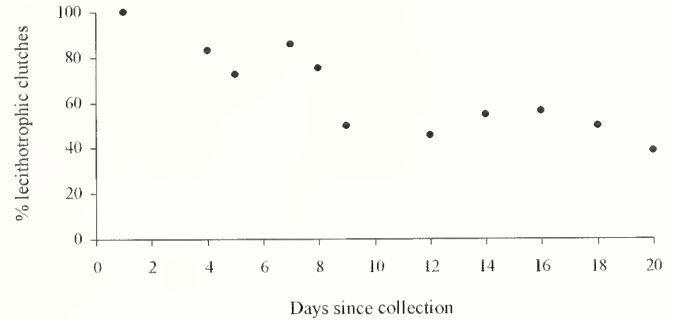


Figure 4. Change in developmental mode expressed by adult *Alderia willowi* following collection from the field. Adults initially produced lecithotrophic larvae when first collected and were maintained on patches of *Vaucheria longicaulis* in the laboratory for three subsequent weeks. Data are the percentage of lecithotrophic clutches produced on a given day out of the total number of egg masses deposited by adult specimens ($n = 25$).

Lecithotrophic veligers are rare in plankton samples above patches of *Vaucheria* spp. (D. Willette and P. Krug, unpubl. obs.), suggesting most metamorphose at or before release. Alternation of developmental modes is thus one dispersal polymorphism, producing long-lived versus short-term larvae in *A. willowi*.

Spontaneous metamorphosis and bet-hedging dispersal strategies in *Alderia willowi*

A second dispersal polymorphism occurs within lecithotrophic clutches of *Alderia willowi*: 0-90% of larvae spontaneously metamorphose prior to emergence or within 2 days of hatching, while their siblings delay settlement until

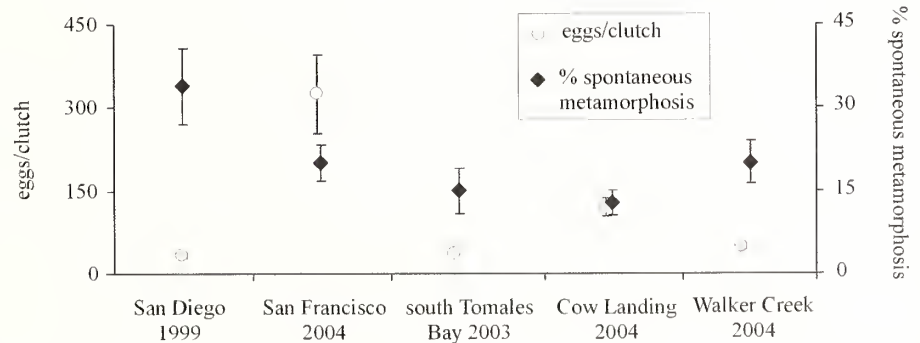


Figure 5. Spontaneous metamorphosis among lecithotrophic larvae of *Alderia willowi* from different years and field sites. Adults were collected from San Diego (August 1999), southern Tomales Bay (September 2003), and from San Francisco Bay, Cow Landing, and Walker Creek (August 2004). Data are percentages of spontaneous metamorphosis (mean \pm SE) occurring over the first 48 hr post-hatching, in the absence of any inductive substratum.

contacting the host alga (Krug 2001). In many species, larvae are more likely to metamorphose spontaneously with age, a "desperate larva" effect (Gibson 1995, Toonen and Pawlik 2001). The case of *A. willowi* stands in contrast: veligers that do not spontaneously metamorphose die over the next 14 days if denied access to the host, contradicting the hypothesis that non-feeding larvae should lose settlement specificity with age.

Although this trait was highly variable among individuals, the San Diego population hovered around a mean of roughly 25% spontaneous metamorphosis over four years (Krug 2001). Data from four additional populations, surveyed from August to September of 1999, 2003 or 2004, showed a similar trend (Fig. 5). The proportion of spontaneous metamorphosis varied significantly among populations (results of a Kruskal-Wallis test: $H = 11.02$, $P < 0.05$) but was uncorrelated with fecundity (Spearman Rank Correlation: $P > 0.30$). Local conditions were highly variable, as reflected in the mean fecundity of different populations, but good conditions did not produce higher levels of spontaneous metamorphosis (Fig. 5). Stabilizing selection could maintain a mean 15-30% spontaneous metamorphosis at most sites and times, even under optimal conditions. The highest mean value (San Diego, 1999) was due to two slugs that produced clutches with >80% spontaneous metamorphosis, reflecting the variable nature of this trait.

Spontaneous metamorphosis among newly hatched larvae acts as a bet-hedging dispersal strategy, retaining some offspring from each clutch in the parental habitat while allowing the remainder to potentially locate a new algal patch. Bet-hedging is a strategy that raises the geometric mean fitness of a genotype by lowering variation in reproductive success year to year (Seger and Brockmann 1987, Phillipi and Seger 1989, Hopper 1999). A middle-of-the-road approach, bet-hedging genotypes trade the benefit of producing a high recruitment cohort under good conditions against the risk of no reproductive success in bad seasons. This makes it likely that some offspring will survive, regardless of environmental fluctuations. Over many generations, such a genotype has a higher relative growth rate than one that fails to reproduce under any given set of conditions.

In most populations of *Alderia willowi*, about a quarter of lecithotrophic larvae metamorphose with an abbreviated planktonic period or none at all; these larvae are likely to survive if local conditions remain favorable in the natal habitat patch. Their siblings disperse until cued to metamorphose by contact with a new patch of algae, and may survive if conditions in the parental habitat deteriorate. Such a strategy maximizes the chance that some offspring will survive, whether local patches of *Vaucheria* spp. persist or die back. The proportion of spontaneous metamorphosis was also phenotypically plastic, decreasing in response to adult star-

vation (Krug 2001). Strategies that vary the spatial or temporal distribution of offspring are known for other taxa including plants (Payne and Maun 1981, Telenius and Torstensson 1989, Imbert 1999), mammals (Gaines and McClenaghan 1980), and insects (Harrison 1980, Bradford and Roff 1993, Zera and Denno 1997, Langelotto and Denno 2001), and may be a common evolutionary response to fluctuating environments (Giesel 1976, McPeck and Holt 1992, Kawecki and Stearns 1993, Chia *et al.* 1996).

Effects of developmental pathway on larval swimming and settlement behavior

From a larval biologist's perspective, poecilogony is a chance to explore how conspecific larval morphs produced by divergent developmental pathways compare behaviorally, especially in their response to physical and chemical stimuli during habitat choice. Studies of other poecilogonous species have focused on the ecological effects of different strategies on adult population dynamics (Levin and Huggett 1990, Morgan *et al.* 1999), but not on larval behavior. Variable development in *Alderia willowi* provides the opportunity to compare competent larvae differing greatly in age and in trophic mode.

Krug and Zimmer (2000, 2004) compared physical properties (size, passive sinking rate) as well as swimming behavior for precompetent planktotrophic larvae and both types of competent larvae (Table 2). Quantitative motion analysis revealed the swimming paths of planktotrophic larvae grow straighter and are increasingly directed downwards as larvae mature; competent stages are larger, and sink and swim faster than early stages. When planktotrophic larvae attain competence, they are the same size as 1-day old lecithotrophic larvae, and sink and swim at a similar speed (Table 2). Both competent morphs also share the same shadow response, suggesting behaviors are conserved across developmental programs (Krug and Zimmer 2004). The primary difference in the two morphs is that lecithotrophic larvae swim downward in straighter paths, resulting in a greater net rate of displacement towards the bottom. Modeling efforts indicate differences in swimming behavior could produce a 5-fold greater rate of contact with the bottom for lecithotrophic larvae under natural flow conditions.

If mature planktotrophic larvae tend to encounter dissolved cues while suspended in the water column, stronger behavioral responses might adaptively increase their odds of recruitment. In contrast, because most lecithotrophic larvae hatch in or near suitable juvenile habitat, selective pressure to respond to dissolved cues could be relaxed for this morph. To test these hypotheses, both types of competent larvae were exposed to algal extract or field-collected conditioned seawater (CSW) from within algal patches. Swimming behaviors were quantified through video motion analysis for

Table 2. Physical characteristics and swimming behavior of planktotrophic and lecithotrophic larvae of varying ages in *Alderia willowi* (Krug and Zimmer 2004). Data are mean (\pm SE) larval size, sinking rate, and swimming behaviors for larvae differing in age and developmental mode. NGD is a ratio of the linear distance from the first to the last point of a given path to the actual distance traveled; a value of zero indicates a circle, whereas a ratio of 1.0 represents a straight line. Vertical speed is a measure of larval movement in the Y-dimension only. Speed is a non-directional scalar, whereas net vertical displacement rate is a vector with negative values indicating downward movement. Behaviors were quantified in the dark using an IR-sensitive video camera.

	Planktotrophic		Lecithotrophic	
	8-d old	32-d old	1-d old	4-d old
Shell size (μ m)	126 \pm 1	194 \pm 1	194 \pm 1	194 \pm 1
Gravitational fall velocity (mm/s)	-0.90 \pm 0.09	-1.59 \pm 0.12	-1.52 \pm 0.10	-0.99 \pm 0.10
Swimming speed (mm/s)	0.85 \pm 0.05	1.03 \pm 0.09	1.21 \pm 0.04	1.32 \pm 0.07
NGD ratio	0.83 \pm 0.03	0.84 \pm 0.02	0.92 \pm 0.01	0.90 \pm 0.03
Vertical speed (mm/s)	0.42 \pm 0.06	0.65 \pm 0.07	0.92 \pm 0.06	0.99 \pm 0.12
Net vertical displacement rate (mm/s)	-0.10 \pm 0.08	-0.40 \pm 0.12	-0.78 \pm 0.09	-0.73 \pm 0.21

larvae suspended in the water or moving along the bottom of an experimental chamber. Larvae of both types respond similarly to dissolved cues, turning more frequently and staying close to where the cue is initially perceived (Krug and Zimmer 2000). Larvae suspended off the bottom significantly decrease their speed, swimming in slow helices instead of the straight lines seen in seawater controls. Along the bottom, larvae swim in tight circles or hop, making frequent contact with the substrate (Krug and Zimmer 2000). Such behaviors should increase the chance of contacting a point source of soluble cues (Tamburri *et al.* 1996). Little difference is evident between the two morphs, indicating that selection has maintained a suite of behaviors in relatively non-dispersing larvae that should enhance opportunities for host colonization.

Upon contact with the host alga or after exposure to dissolved cues, larvae attach to the substrate with the propodium (settlement) and begin metamorphosis. Competent larvae of both morphs are equally host specific, settling in response to *Vaucheria longicaulis* but not other macroalgae (Krug and Zimmer 2004). When tested with lecithotrophic larvae, host specificity in *Alderia willowi* is higher than that of any other sacoglossan studied to date, with >90% metamorphosis on *V. longicaulis* but no significant response (0-10%) to 16 alternative algae or mudflat sediments (Krug 2001). Specificity for *V. longicaulis* does not diminish with age (Krug 2001). Such specificity is not found among anaspidean opisthobranchs, which can be stenophagous as adults but settle less specifically as larvae; >30% of *Aplysia californica* larvae metamorphosed on 10 different macroalgae and >25% of *Aplysia oculifera* settled on 4 of 12 tested macroalgae (Pawlik 1989, Plaut *et al.* 1995). Sacoglossans restricted to a single genus or species of host algae often settle specifically on the obligate adult food, reflecting a high degree of

coevolution (West *et al.* 1984, Krug 2001, P. Krug, unpubl. obs.).

Dispersal period and rate of metamorphosis

Larvae of *Alderia willowi* vary in their rate of metamorphosis according to age. Larvae of all ages settle within 1-2 hr of exposure to *Vaucheria longicaulis*, but young lecithotrophic larvae (1-2 days post-hatching) delay metamorphosis relative to older larvae (Botello and Krug 2006). About 50% of 1- or 2-day old lecithotrophic larvae complete metamorphosis after 24 hr, but 90-100% response requires 48 hr (Fig. 6). In contrast, 4-day old lecithotrophic larvae metamorphose at an accelerated rate, with >90% of metamorphosis occurring in the first 24 hr of exposure to the host (Fig. 6). Young larvae rarely metamorphose in the first 12 hr after settlement, but a substantial fraction of older lecithotrophic larvae metamorphosed in <12 hr (Botello and Krug 2006). Previously unpublished data show that competent planktotrophic larvae behaved like older lecithotrophic larvae, with most metamorphosis occurring in the first 24 hr (Fig. 6). Thus, in both morphs, longer-lived larvae metamorphose faster after settling on the host.

The increased rate of metamorphosis among older lecithotrophic larvae may be a response to diminishing yolk reserves; 1-2 day old larvae can energetically afford to delay metamorphosis for 12-24 hr while evaluating their surroundings, whereas some older larvae die after 5 days (Krug 2001). The results for competent planktotrophic larvae can be similarly interpreted as an adaptive response, as larvae that have survived a perilous month at sea are under strong pressure to locate a patch of *Vaucheria* without further risk of planktonic mortality. Because competent planktotrophic larvae were fed prior to the assay, they were not energetically constrained as were the 4-d old lecithotrophic larvae; it

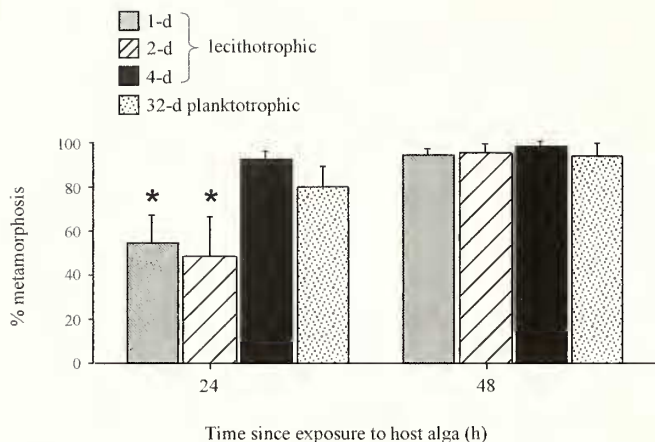


Figure 6. Rate of metamorphosis for different larval morphs of *Alderia willowi*. Cumulative percentages of metamorphosis following exposure to the adult host alga are plotted for lecithotrophic larvae of varying ages (data from Botello and Krug 2006) vs. competent, 32-day old planktotrophic larvae. For each age class, percent metamorphosis after 24 vs. 48 hr was compared using a Wilcoxon Signed-Rank test to determine if less metamorphosis occurred during the first 24 hr period; *, $P < 0.05$.

therefore appears that metamorphic rate varies according to the life history of a larva, as well as to individual energy levels. Larvae differing widely in age thus have similar patterns of host specificity and settlement behaviors, but differ in rate of metamorphosis depending on an individual's dispersal history.

CONCLUSIONS AND FUTURE DIRECTIONS

The developmental plasticity previously attributed to *Alderia modesta* in fact occurs within its sister species, *Alderia willowi*. Specimens of *A. willowi* can vary the developmental mode of their larvae, alternating seasonally between lecithotrophy and planktotrophy, which is unprecedented among poecilogonous polychaetes and gastropods. Ongoing research aims to unravel the environmental cues that trigger changes in development, which in turn may shed light on the evolutionary forces that favor lecithotrophy in the southern species. Within lecithotrophic clutches of *A. willowi*, a second dispersal polymorphism exists: some larvae spontaneously metamorphose at hatching, while their siblings disperse until stimulated to metamorphose by dissolved or surface-bound carbohydrates from the host alga *Vaucheria longicaulis*. The proportion of spontaneous metamorphosis is highly variable between individuals but the population mean rarely exceeds 25%, even when conditions are optimal. Stabilizing selection might maintain this level to produce a

bet-hedging effect, with a quarter of all offspring recruiting into the parental population and the rest dispersing until an algal patch is encountered. The alternative developmental pathways in *Alderia willowi* converge to make a similar competent larva; although differing in age by >30 days, both morphs swim and sink at similar rates, and alter their swimming behavior in response to habitat cues in ways predicted to increase the likelihood of successful recruitment. The rate of metamorphosis, however, changes according to the developmental history and energy level of a given larva.

As biology moves into the proteomic era, poecilogonous species offer the chance to investigate proximal mechanisms such as changes in gene regulation and maternal effects that underlie alternative developmental pathways. Transitions between developmental modes have occurred frequently in many invertebrate taxa, yet stable expression of multiple developmental morphs is vanishingly rare, a paradox waiting to be resolved. The study of poecilogonous species like *Alderia willowi* should provide a more complete understanding of how the interplay between adult and larval ecology shapes adaptive evolution of marine life histories.

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